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The Ecology of Atlantic Cod (*Gadus morhua*) in Canadian Arctic Lakes

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ABSTRACT. The range of limnological conditions that support Atlantic cod populations in meromictic Arctic lakes is known to be relatively restricted. The degree to which differences in these features, particularly in the availability of allochthonous and autochthonous prey, affect the condition and growth of cod in these populations is unknown. We compared measures of condition among three Atlantic cod populations on Baffin Island, Nunavut, to assess their relationship to differences in potentially important habitat parameters. We also compared data spanning two decades (Ogac Lake) to five decades (Qasigialiminiq) to assess the degree to which natural and anthropogenic factors may have affected these populations. In general, growth rate and asymptotic length tend to be high under situations of intense cannibalism and when alternative prey species are relatively abundant. Biotic and abiotic habitat features in Ogac Lake appear to have been relatively stable since the 1950s, although the abundance of sea urchins appears to have decreased, which may explain the observation that the incidence of cannibalism has doubled. The mean size of angled cod in Qasigialiminiq has decreased by about 10 cm over the past 20 years.

Key words: landlocked Atlantic cod, cannibalism, Arctic, meromictic lakes, growth comparisons, condition factor comparisons, diet comparisons

RÉSUMÉ. L'étendue des conditions limnologiques qui soutiennent les populations de morue franche dans les lacs méromictiques de l'Arctique est reconnue pour être relativement restreinte. La mesure dans laquelle les différences caractérisant ces conditions a une incidence sur l'état et la croissance des morues n'est pas connue, particulièrement en ce qui a trait à la disponibilité de proies allochtones et autochtones. Nous avons comparé les mesures des conditions de trois populations de morues de l'île de Baffin, au Nunavut, dans le but d'évaluer leur relation avec les différences caractérisant des paramètres d'habitat susceptibles d'être importants. Nous avons également comparé des données s'étendant sur deux décennies (lac Ogac) à cinq décennies (lac Qasigialiminiq) pour évaluer la mesure dans laquelle les facteurs naturels et anthropogéniques pourraient avoir une incidence sur ces populations. En général, le taux de croissance et la longueur asymptotique ont tendance à être élevés dans les situations de cannibalisme intense de même que lorsque les espèces de proies de rechange sont relativement abondantes. Les caractéristiques des habitats biotiques et abiotiques au lac Ogac semblent relativement stables depuis les années 1950, bien que l'abondance d'oursins semble avoir diminué, ce qui pourrait expliquer l'observation selon laquelle le cannibalisme a doublé. La grosseur moyenne de la morue prise à la ligne au lac Qasigialiminiq a diminué d'environ 10 centimètres ces 20 dernières années.

Mots clés : morue franche des lacs, cannibalisme, Arctique, lacs méromictiques, comparaisons de croissance, comparaisons de facteurs de conditions, comparaisons de régimes alimentaires

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INTRODUCTION

The tendency of individuals and populations at the edges of species' ranges to exhibit extreme or unusual phenotypes relative to their centrally adapted counterparts is likely related to the fact that the abiotic, biotic, and interacting components of peripheral habitats tend to approach species' tolerance limits (Gaston, 2003). The Atlantic cod (*Gadus morhua*) populations in Ogac Lake (OG), Qasigialiminiq (QL), and Tariujarusiq (TL) on Baffin Island, Nunavut, Canada (Fig. 1), persist in highly unusual habitats for the species at the biological and geographical limits of its range (Hardie et al., 2008). Between the freshwater surface layer and the hypersaline anoxic depths of each lake lies what is essentially a band of suitable seawater habitat, the extent and nature of which depend greatly on the magnitude and frequency of tidal and freshwater inflows and local topography.

Low species diversity of vertebrates and invertebrates, with the physiological stressors associated with depressed temperature and salinity, suggests that the frequency and volume of tidal inflows may strongly affect the overall condition of these extreme populations by maintaining salinity and providing allochthonous nutrition. Local knowledge

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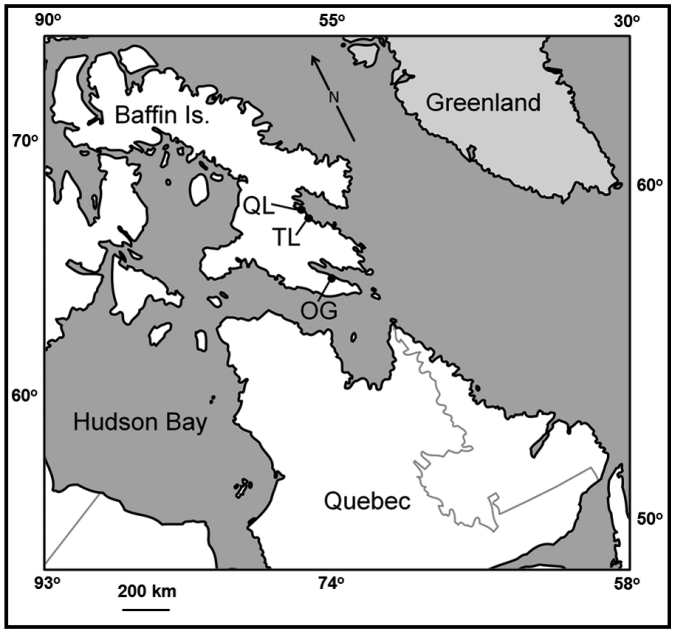

FIG. 1. Map showing the approximate locations of three landlocked Altantic cod populations in coastal meromictic lakes on Baffin Island, Nunavut, Canada.

(Iqaluit) suggests that the river connecting OG to Frobisher Bay remains open throughout the winter in some years, whereas the connections between both QL and TL and Cumberland Sound freeze solid. The fact that tidal inflows continued throughout the winter of 2004–05 in OG, but not in the winters of 2003–05 in TL, supports this suggestion (Hardie et al., 2008). Observations (Kennedy, 1953) and quantification (Hardie, 2004) of significant inflows of allochthonous nutrients and the intense feeding on these resources by cod suggest that the cod in OG benefit strongly from these inflows. Similar influxes of allochthonous nutrition have not been verified at QL or TL, where tidal inflows are less frequent, smaller in volume, and less forceful (Hardie et al., 2008). These three factors are likely to result in smaller influxes of marine organisms per tide and overall into the latter two lakes.

The diets of cod in marine waters include a broad array of invertebrate and vertebrate items (Waiwood and Majkowski, 1984; Lee and Khan, 2000). Cod diet composition is known to have important effects on growth and condition (Grant et al., 1998; Schwalme and Chouinard, 1999), which in turn impinge on individual fitness and population dynamic parameters (Rakitin et al., 1999, 2001; Dutil and Lambert, 2000), as in other species (Hedrick et al., 1976). Aside from other cod, the principal prey items for cod in these lakes are three benthic species: the clam, *Saxicava arctica*, which persists at or near the interface between the upper freshwater layer and the middle seawater layer; the sea urchin, *Strongylocentrotus droebachiensis*, which persists throughout the seawater layer; and the coneworm (polychaete), *Pectinaria granulata*, which occurs at or just below the interface between the seawater and the anoxic, hypersaline bottom layers. Cod must venture into low-salinity environments to forage for clams, and into hypersaline and poorly oxygenated parts of the water column for coneworms. In such environments, Atlantic cod are known to incur significant physiological costs (Claireaux et al., 1995). This factor may be particularly important in QL, where the absence of sea urchins (Hardie et al., 2008) may force non-cannibalistic cod to forage exclusively in these physiologically stressful environments at the top and bottom of the water column.

Patriquin (1967) and Lewis (1989) summarized data from previous research at Ogac Lake (1952, 1957, 1962) and Qasigialiminiq (1985, 1986), and we have been able to extract some raw data from field notes and collections made available to us for those years, as well as for 1989 at QL and 1999 at OG. Although the time span between these studies and our research is not great (20–50 years), habitat changes in both lakes may have been significant. First, rapid glacio-isostatic rebound in this area of Baffin Island has caused the frequency and volume of tidal inflows to decrease, perhaps dramatically so (Hardie et al., 2008). Second, the current climate-warming trend (Wookey, 2007) may have important effects on abiotic and biotic aspects of the habitat at these two lakes via increased temperatures, diminished snow and ice cover, extended open-water seasons for tidal inflows, and other unforeseen effects.

Hardie et al. (2008) reviewed the shared and divergent abiotic and biotic features of these three Arctic lakes and several others in which cod populations persist, examining the extent, frequency, and nature of tidal inflows, the extent of lake temperature and salinity stratification, and species composition. In this paper, we examine how these abiotic and biotic features, as well as lake bathymetry, cod stomach contents, and prey lipid content, relate to various measures of condition at both individual and population levels within and among the Baffin Island lakes. These metrics include frequency distributions for length and age, condition metrics (hepatosomatic index, condition factor, length-weight relationship), sex ratios, ages and lengths at maturity, and von Bertalanffy growth parameters k (growth rates) and L_∞ (asymptotic lengths).

We test the hypothesis that the above differences in forage availability and stomach contents in the three lakes on Baffin Island will result in a gradient of cod condition and growth parameters (growth rate and asymptotic length). We expect that OG cod will exhibit the highest condition factors and growth parameters because of perennial inflows of allochthonous nutrients to OG and its higher diversity of benthic species than in QL or TL; that QL cod will be in the poorest condition and grow the least quickly because of their limited allochthonous nutrition and the absence of sea urchins; and that TL cod will hold the intermediate position. Secondly, we compare these data to previous research data (length frequency distributions, condition metrics, sex ratios, age/length at maturity) from OG and QL to hypothesize the possible effects of habitat changes linked to glacio-isostatic rebound, climate warming, or both on these populations.

METHODS

Bathymetry and Limnology

Bathymetric contours were approximated by taking depth measurements at 15-second intervals along transects between identifiable topographical features across the lakes (inflows, outflows, points, bays, islands, etc.) from a boat moving at constant velocity. Depths along each transect were transcribed to a map of the lake. The number of transects and the distance between transects was limited by the number of identifiable topographical features on each side of the lakes, but in no instance did the distance between approximately parallel transects exceed 500 m. Two approximately perpendicular sets of transects were measured for QL and TL. Bathymetric information for OG is modified from McLaren (1967). Biotic limnological observations and collections were made using underwater video apparatus for qualitative benthic species composition and cod feeding observations (Nature Vision, Inc., Brainerd, Minnesota); coarse (330 μm) and fine (70 μm) mesh 50 cm diameter plankton nets for qualitative analysis of ichthyoplankton and invertebrate plankton; and a small, manually operated benthic drag (42 cm × 22 cm opening, 1.2 cm mesh) for qualitative benthic species composition analysis.

Cod Sample Collection

Specimens were collected using hook and line, gill nets, and minnow traps at all three lakes (Ogac, Qasigialiminiq, Tariujarusiq) in July and August 2003, and again at Ogac Lake in July and August 2004 and July 2005. Sinking gill nets used were 2.5 m × 15 m dimensions hung with monofilament netting in 2.5, 3.75, 5, and 6.5 cm mesh (Redden Net Co. Ltd., Campbell River, British Columbia) and were fished on the bottom in the seawater layer at depths ranging from 5 to 30 m for set times ranging from 5 to 60 minutes. Length data from cod previously collected at OG (n = 45, 1999) and QL (n = 25, 1985; n = 104, 1986; n = 100, 1999) were obtained from Fisheries and Oceans Canada, Iqaluit, Nunavut.

Stomach Contents

Stomach contents were assessed from lethal samples and by gastric lavage and enumerated to order/species. Unidentifiable material was excluded. The taxonomic composition of the stomach contents was qualified as consisting of seaurchin, brittle-star, amphipod, mysid, decapod, polycheate worm, coneworm, larval fish, or Atlantic cod. Individuals were classified as cannibals if they had any part of a juvenile or adult cod in their stomachs, including otoliths. The length at onset of cannibalism (the predicted length at which 50% of cod begin to prey on their conspecifics) was calculated by logit analysis.

Prey and Cod Tissue Lipid Content

Wet-weighed whole bodies of common prey items were collected from the lakes (not from stomach contents) and preserved in a 2:1 chloroform-methanol mixture in the field. The lipid content of different prey types was assessed using methods described by Budge et al. (2006).

Cod Condition and Maturity

The hepatosomatic index (HSI) and condition factor (*K*) were calculated using lethal samples from all three populations, as follows:

$$HSI = 100 \cdot \text{liver weight (g)} \cdot \text{round weight (g)}^{-1} \quad (1)$$

$$K = 100 \cdot \text{round weight (g)} \cdot \text{total length (cm)}^{-b} \quad (2),$$

where b is the exponent of the length-weight relationship (equation 4).

Maturity was assigned by macroscopic observation of cod gonads in the field, following the scheme of Templeman et al. (1978). Size and age at maturity were calculated by logit analysis, as the predicted lengths and ages at which 50% of cod of each sex are mature in each population.

Age Estimation

One sagittal otolith from each individual (n = 447) and all otoliths found loose in stomach contents were sectioned and resin-mounted at the Otolith Research Laboratory (2011) of the Bedford Institute of Oceanography in Dartmouth, Nova Scotia. For sectioned otoliths that were difficult to read or appeared not to have been sectioned through the nucleus (53/447), the second sagittal otolith was broken by hand and wet-polished on emery cloth (200–800 grit) mounted on a plexiglass sheet. Digital images of both types of otolith preparations were captured with a Nikon DXM1200 camera mounted on a Nikon C-DSD115 stereo microscope under reflected light, using the image analysis program ACT 1 (Nikon Instruments Inc., Melville, New York). Digital images of magnified otoliths were manipulated using Photoshop 7.0 (Adobe Systems Incorporated) to optimize the contrast between opaque and hyaline zones (interpreted as representing summer and winter growth periods, respectively).

Although age validation was not possible for these populations, several measures were taken to ensure the best possible interpretation of otolith annular patterns. A subsample of otoliths was aged by experts at the Marine Research Institute, Reykjavik, Iceland. Overall, 49 of 213 age interpretations differed from those of the authors; of these, 39 (80%) differed by only one year, and the largest difference was three years. The linear regression of our data against age estimates from the Marine Research Institute suggests no systematic bias (Table 1).

TABLE 1. Summary of the linear regression of the authors' age estimates against age estimates from the same otoliths by researchers at the Iceland Marine Research Institute (Reykjavik).

Population	n	Slope	*p*-value	r	Mean age estimate difference ± SE
Ogac Lake	112	0.96	< 0.00001	0.98	-0.13 ± 0.05
Qasigialiminiq	48	0.90	< 0.00001	0.95	0.04 ± 0.09
Tariujarusiq	51	0.94	< 0.00001	0.96	-0.04 ± 0.09

For all statistical analysis, we used the R software for statistical computing (version 2.5.1; R Development Core Team, 2005) and SAS (1999) statistical analysis software.

Back Calculation of Length-at-Age

We tested four different nucleus-to-margin otolith transects (anterior, posterior, dorsal, and ventral) to verify the proportionality of otolith length to fish length. A transect through the ventral plane of the otolith (Fig. 2) yielded a strong linear relationship between otolith and fish length for all three populations (r = 0.81–0.88, all $p <$ 0.0001). Relative inter-annular distances were digitized, starting from a landmark at the center of the nucleus and placing subsequent landmarks at the start of each opaque summer growth zone, using the programs tpsDig2 and tpsUtil (Rohlf, 2004, 2005). Relative distances were converted to absolute distances (mm) to apply the biological intercept method (all lengths in mm, Campana, 1990), using a published biological intercept value for Atlantic cod from Sinclair et al. (2002). These values were converted to back-calculated lengths-at-age using the equation:

$$L_a = L_c + (O - O_c)\,(L_c - L_i)\,(O_c - O_i)^{-1} \qquad (3),$$

where L_a is the estimated length at age a, L_c is the length at capture, O is the distance from the centre of the nucleus to the outer edge of the opaque annulus corresponding to age a, O_c is the distance from the centre of the nucleus to the outer edge of the otolith, and L_i and O_i are the fish length (2.44 mm) and otolith length (0.44 mm) at the biological intercept (Sinclair et al., 2002).

Length-Weight Relationship

A power model was fit to the length and weight data for each population to obtain nonlinear least-squares estimates of the parameters of a nonlinear model relating length and weight for each of the three populations:

$$W = a \cdot L^b \qquad (4)$$

using starting values of a = 0.001 and b = 3 (isometric growth).

The length-weight (L-W) relationships in the three populations were examined in three pairwise comparisons, using a nonlinear model:

$$W = (a_1 + a_2) \cdot L^{(b_1 + b_2)} \qquad (5)$$

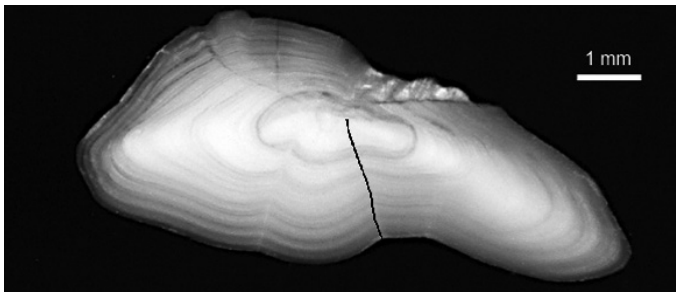

FIG. 2. A cross-section of the sagittal otolith of an Atlantic cod (age = 8 years). The distance from the nucleus to the ventral side of sectioned otoliths along the transect shown has a strong linear relationship to total length and provided a clear view of annuli in cod from all three populations in this study. (The transect is drawn to cross each annulus approximately perpendicularly and is therefore not straight.)

where a_1 is the intercept for one population and a_2 is the difference in the intercepts between populations 1 and 2. If a_2 is significant, then there is a significant difference between the two populations for the intercept term. The same applies to b_1 and b_2, which are the slopes of the L-W relationship for population 1 and the difference in the slopes of the L-W relationship between populations 1 and 2, respectively.

Population Growth Comparisons

In order to account for the non-independence (serial correlation) of lengths-at-age back-calculated from otolith annulus measurements, we used a non-linear mixed effect (NLME) approach to fit a classic von Bertalanffy growth model (VBGM) to the data for each of the three populations:

$$L_{a,i} = (\mu L_\infty + L_{\infty,i})(1 - \exp(-(\mu k + k_i)(t_{a,i} - \mu t_0 + t_{0,i}))) \qquad (6)$$

where $L_{a,i}$ is the predicted length of individuals i at age a; μL_∞ is the mean VBGM asymptotic length parameter, and $L_{\infty,i}$ is the deviation from μL_∞ of the asymptotic length for individual I; μk is the mean VBGM growth parameter, k_i is the deviation from μk of the growth parameter for individual i; $t_{a,i}$ is the size at hatch of individuals i at age a; μt_0 is the mean VBGM age-at-hatch parameter, and $t_{0,i}$ is deviation from μt_0 of the age-at-hatch for individual i. The overall VBGM and the k, L_∞ and t_0 parameters were compared between each pair of populations (i.e., OG-QL, QL-TL, OG-TL) using the NLMIXED procedure in SAS (SAS Institute Inc., 1999) to apply the maximum likelihood test described by Kimura (1980), as recommended for the analysis of annulus-based size-at-age data (Schaalje et al.,

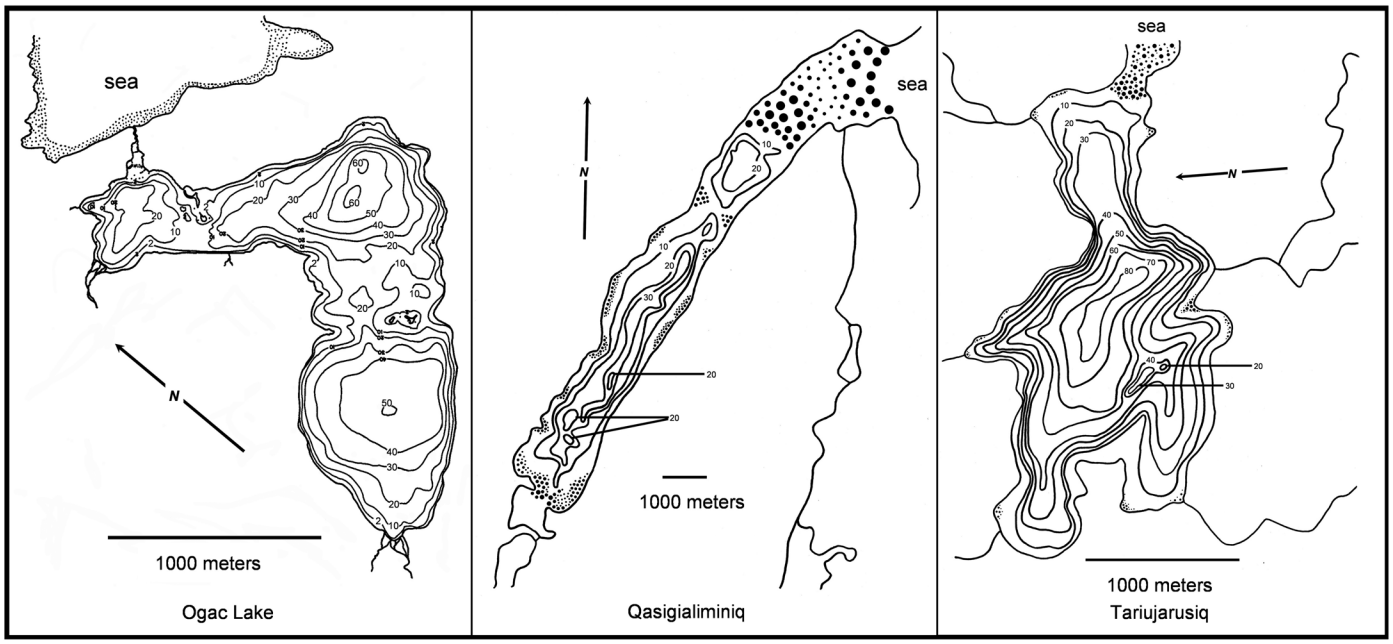

FIG. 3. Bathymetry of Ogac Lake (adapted from McLaren, 1967), Qasigialiminiq, and Tariujarusiq. The solid circles indicate ridges of gravel and boulders.

2002). This method compares models using likelihood ratio tests. For example, to test the difference in L_∞ between two datasets (e.g., populations or sexes), one can compare the likelihood of an unconstrained model with separate values for all three parameters to the likelihood of a constrained model assuming a common L_∞. If the likelihoods of the two models differ significantly, then the L_∞ parameter differs significantly between the two datasets. The same approach was used to compare growth between sexes for OG.

RESULTS

Biotic Limnology and Stomach Contents

The three study lakes show important qualitative differences in bathymetry, hydrography, and limnology. Notably, the nature of their connection to the sea differs greatly (Fig. 3), which may have significant biological consequences (Hardie et al., 2008).

Important qualitative differences in the stomach contents of cod were also found in the three lakes (Table 2). Most notably, echinoderms (sea urchins and brittle stars) were absent from stomachs in QL, in contrast to their prevalence in OG and particularly in TL samples, where they were found in the stomachs of one-third of the cod over 20 cm long. In general, cod in OG consumed a greater diversity of benthic prey, and exhibited more than double the incidence of cannibalism found in cod in QL or TL. We observed cannibalized individuals from 10 to 36 cm long in the stomachs of cod in 2003–05, and cannibalized cod lengths back-calculated from otoliths found in cod stomachs ranged from 8.7 to 23 cm. The smaller maximum size identified through back-calculation could have been due to otolith abrasion in cod stomachs or predation on unusually large cod as a result of our field sampling (i.e., depredation of angled/netted/released cod), or both.

Patriquin (1967) reported the percentages of cod in three length groups (14–22 cm, 30–49 cm, > 50 cm) that were found to contain each of seven dietary items in their stomachs, as well as the percentage in each group observed with empty stomachs. Our data from 2003–05 showed no great change from Patriquin's figures in the frequency of occurrence of most prey items (Table 3), with two dramatic exceptions: the frequency of sea urchins had decreased by more than half, and cannibalism had nearly doubled. Furthermore, Patriquin (1967) reported that only cod between 20 and 40 cm were found to be victims of cannibalism. In contrast, we found in 2003–05 that smaller cod from 8.7 to 36 cm in length were also preyed upon (excluding cannibalism on recently tagged/released fish, which ranged up to 62.4 cm). The predicted length at which 50% of fish in each population began cannibalistic feeding was 61.5 cm in OG, 63.2 cm in QL, and 87.5 cm in TL.

The most lipid-rich prey items (larval cod – 5.25% lipid) had 16 times the fat content of the most lipid-poor prey items (clams – 0.32% lipid) (Fig. 4). Lipid contents differed significantly between two groups of prey items: (1) larval cod, larval sculpin, and polycheate worms and (2) all other prey items (ANOVA, $p \sim 0$, Tukey's HSD test). Larval cod, larval sculpin, and polycheate worms did not differ significantly from each other (all $p > 0.34$), but had significantly higher lipid contents than all other prey items (all $p < 0.02$), which also did not differ significantly from each other (all $p > 0.13$). Although amphipods, decapods, and mysids were frequently found in the stomachs of cod from all three lakes (21–45%), by mass they made up only a small part of most stomach contents. In contrast, clams, coneworms, and sea

TABLE 2. Frequency of occurrence of prey items found in the stomachs of Atlantic cod from Arctic lacustrine populations. Percentages are based on the sample sizes given in the column title for each lake, with the following exceptions. Stomach contents of cod larger than 20 cm are considered for all prey items except conspecifics (cannibalism), for which only cod longer than 37 cm (minimum length of observed cannibals) are considered. Sculpin larvae are quantified only for samples collected on days when tidal inflows occurred. For brevity, only prey found in more than 5% of stomachs in at least one population are listed in this table, although more species are included in lipid content analysis.

Stomach contents	% Lipid	Ogac Lake (160) %	Qasigialiminiq (104) %	Tariujarusiq (92) %
Juvenile cod (*Gadus morhua*)	1.34	(42/131) 32.06	(13/103) 12.62	(13/92) 14.13
Sea urchins (*Strongylocentrotus droebachiensis*)	0.72	(36) 22.25	–	(31) 33.70
Coneworms (*Pectinaria granulata*)	0.41	(30) 18.75	(42) 40.00	(6) 6.52
Clams (*Hiatella arctica*)	0.32	(15) 9.38	(25) 24.04	(12) 13.04
Amphipods/decapods/mysids	–	(47) 29.38	(22) 21.15	(41) 44.57
Sculpin larvae (*Icelus* & *Myoxocephalus* spp.)	–	(7/98) 7.14	–	–
Brittle stars (*Amphiura* & *Ophiacantha* spp.)	1.15	(11) 6.88	–	(4) 4.35
Jellyfish (Cnidaria) & comb jellies (Ctenophora)	–	(11) 6.88	(3) 2.89	(1) 1.09
Empty	–	(30) 18.75	(34) 32.69	(25) 27.2

urchins were the dominant non-fish prey found in most cod stomachs, so it is noteworthy that these prey had the lowest lipid content.

Length and Age Distributions of Angled Cod

The mean length of angled cod in OG and TL did not differ significantly in 2003, but was about 4 cm greater than that of cod in QL (Table 4, ANOVA, Tukey HSD test, $p < 0.001$; Fig. 5). Median length values were largest in TL, followed by QL, and smallest in OG. This pattern may reflect the influence of a few very large individuals on the mean lengths of OG and TL cod, given that length frequency distributions for both groups showed some evidence of bimodality (Fig. 5).

Mean and median cod lengths in OG showed an increasing trend over time, with a significant difference between the 1950s and 1999–2003 (Table 4, ANOVA, Tukey HSD test, $p < 0.05$; Fig. 6). There was some evidence in support of a bimodal distribution of cod captured, the first (and more numerous group) distributed around 40–60 cm, and the second composed of a small number of giant cod (over 100 cm long). This trend was evident for all years in OG and in TL.

The opposite trend was apparent in QL, where mean and median lengths of angled cod had decreased in recent decades. The mean length of angled cod in QL decreased significantly between 1985–86 (combined mean) and 1989, and again between 1989 and 2003, by a total of nearly 10 cm (Table 4, ANOVA, Tukey HSD, $p < 0.01$, Fig. 7), which is consistent with several independent observations (A. Alikatuktuk and A. Papatsie, pers. comm. 2003).

The mean age of angled cod in 2003 was largest in OG, followed by QL, and smallest in TL (Fig. 8, ANOVA, Tukey HSD test, $p < 0.001$). While the ages of cod from OG and QL appeared to have a normal distribution, the TL distribution appeared skewed toward younger ages, despite the occurrence of large individuals within the sample.

Because the raw length-at-age data used in Patriquin (1967) were not available, we were not able to compare growth rates between the two datasets. However, the comparison of length ranges at age for the two datasets suggested that, in general, length-at-age range was greater among older cod in this study (Table 5).

TABLE 3. Percentages of cod with food in stomachs in which various food items were found (at any abundance) by Patriquin (1967)[1] and in the present study.[2]

	30.0–49.9 cm cod		> 50.0 cm cod	
	Patriquin (1967)	This study	Patriquin (1967)	This study
Coneworms	25.0	28.8	5.7	10.6
Amphipods	15.0	18.8	13.0	13.6
Molluscs	15.0	13.8	15.0	7.6
Sea urchins	67.0	22.5	60.0	24.2
Brittle stars	7.7	10.0	5.8	4.5
Small fish	3.8	8.8	–	10.6
Cod	–	6.3	21.0	54.5
Empty	7.0	20.0	10.0	13.6
No. examined	59	80	62	66

[1] Samples collected in 1951, 1952, 1957, and 1965.
[2] Samples collected in 2003–05.

Cod Condition (HSI, K, L-W)

The mean hepatosomatic index of mature males was significantly higher in QL than in TL and OG (ANOVA, all $p < 0.01$) (Table 6). Conversely, the mean condition factor K was significantly higher in OG and TL than in QL (ANOVA, all $p < 0.01$).

The length-weight relationships for the three populations were described by the following equations:

$$\text{Ogac Lake} \quad W = 0.0022 \cdot L^{3.30} \tag{7}$$

$$\text{Qasigialiminiq} \quad W = 0.0025 \cdot L^{3.49} \tag{8}$$

$$\text{Tariujarusiq} \quad W = 0.0010 \cdot L^{3.26} \tag{9}$$

There was no significant difference between the L-W equations for OG and QL or OG and TL, although QL and TL differed significantly for both parameters ($p < 0.02$).

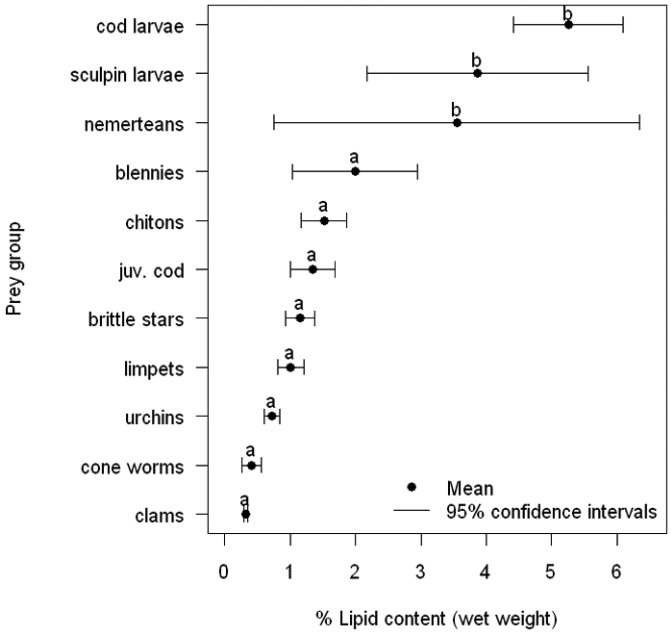

FIG. 4. Percent lipid content (± SE) measured in homogenized whole-bodies of cod prey items collected in July and August in Ogac Lake, Qasigialiminiq, and Tariujarusiq. Letters indicate significantly different lipid concentrations (ANOVA, Tukey HSD test, $\alpha = 0.05$).

TABLE 4. The mean, median, minimum, and maximum total lengths (cm) of angled cod from Ogac Lake, Qasigialiminiq, and Tariujarusiq.

	Year	Mean	Median	Min	Max	n
Ogac Lake	1952	49.1	39	27	141	59
	1957	46.8	43.5	25	111	330
	1999	56	50.5	38.3	110.8	42
	2003	56	47	28	133	241
Qasigialiminiq	1985	61	58	51	102.4	25
	1986	63.1	63	45.4	77.4	104
	1989	54.2	52.5	40	100	100
	2003	51.3	50.5	36	82.3	318
Tariujarusiq	2003	55.4	52.3	29.6	110.7	117

In contrast to the results of Patriquin (1967), who calculated a L-W relationship for cod from OG with an exponent of 3.08 for cod longer than 40 cm, these data from 2003–05 yielded a much higher exponent overall (3.30). When subdivided at 40 cm, they yielded L-W exponents of 2.78 for cod up to 40 cm long and 3.30 for cod longer than 40 cm.

The L-W relationship calculated from Lewis's (1989) data yielded the following relationship:

$$W = 0.00007 \cdot L^{4.16} \qquad (10)$$

which differed significantly from the equation calculated from the 2003 data ($p \sim 0$ for both a and b). Clearly, the length exponent of 4.16 in the L-W equation for Lewis's data predicts strongly positive allometric growth, even more so than the (already high) exponent from this study. However, it should be noted that the intercept from Lewis's data was

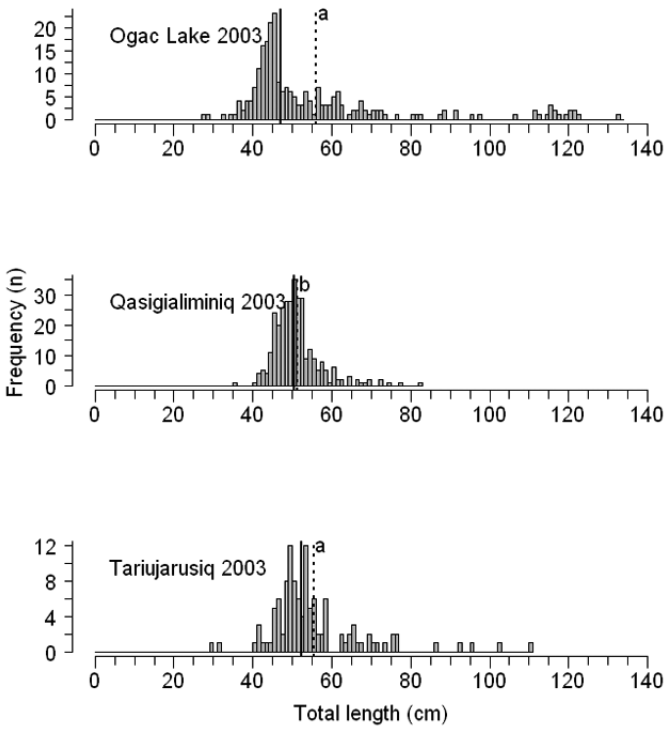

FIG. 5. Length-frequency distributions of cod angled from OG (n = 97), QL (n = 100) and TL (n = 72) in 2003. Median (solid line) and mean (dashed line) values are indicated, and letters indicate significantly different mean lengths (ANOVA, Tukey HSD test, $\alpha = 0.05$).

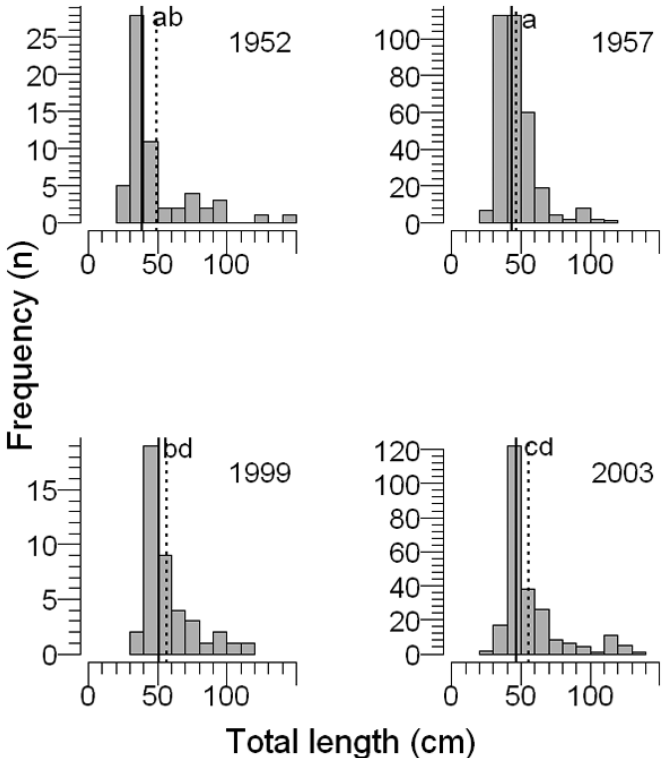

FIG. 6. Length-frequency distributions of cod angled in Ogac Lake in four years between 1952 and 2003. Median (solid line) and mean (dashed line) values are indicated, and letters indicate significantly different mean lengths (ANOVA, Tukey HSD test, $\alpha = 0.05$).

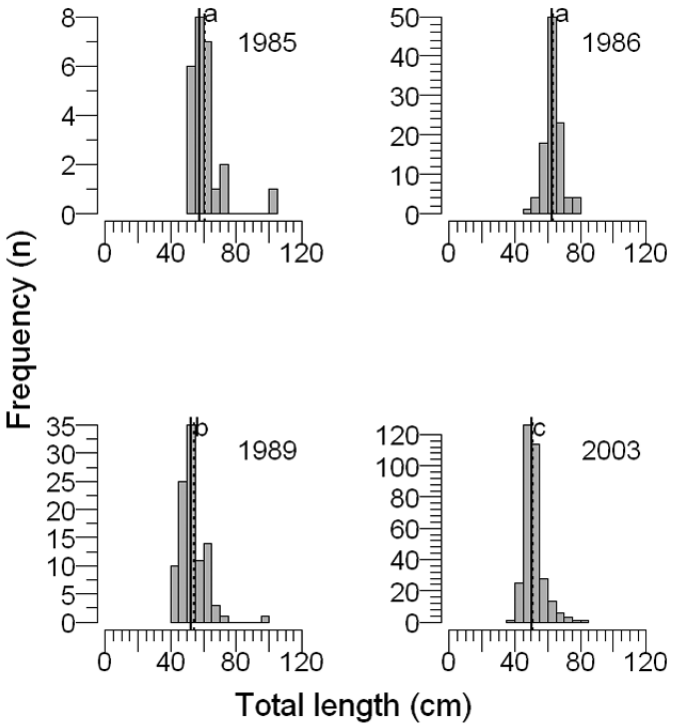

FIG. 7. Length-frequency distributions of cod angled in Qasigialiminiq in four years between 1985 and 2003. Median (solid line) and mean (dashed line) values are indicated, and letters indicate significantly different mean lengths (ANOVA, Tukey HSD test, $\alpha = 0.05$).

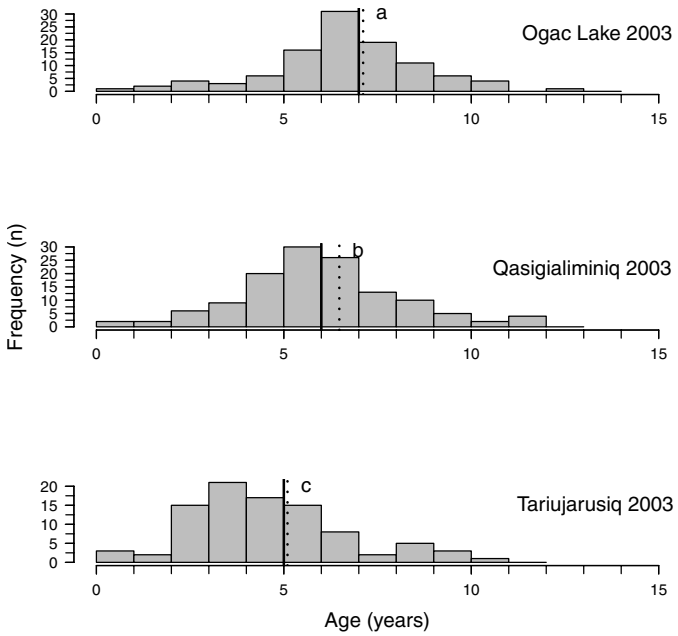

FIG. 8. Age frequency distributions of cod angled in Ogac Lake, Qasigialiminiq, and Tariujarusiq in 2003. Median (solid line) and mean (dashed line) values are indicated, and letters indicate significantly different mean ages (ANOVA, Tukey HSD test, $\alpha = 0.05$).

TABLE 5. Length-at-age extremes (cm) from our data for Ogac Lake (2003–05) compared to data from Patriquin (1967).

	This study		Patriquin (1967)	
Age (years)	Min	Max	Min	Max
1	7.3	16.9	6	17
2	18.5	23.4	13	34
3	22.9	39.7	21	45
4	29.9	48.2	23	56
5	26.5	71.5	27	65
6	37.6	75.5	29	74
7	36.4	107.0	31	90
8	49.5	91.8	33	91
9	46.0	121.0	33	92
10	45.5	118.0	40	101
11	51.6	133.0	40	109
12	–	–	58	112
13	115.4	115.4	60	118
14	–	–	62	126
15	–	–	64	128
16	–	–	66	128
17	–	–	135	141

TABLE 6. Comparison of condition indices for immature and mature cod from Ogac Lake, Qasigialiminiq, and Tariujarusiq.

Lake / maturity	HSI	*K*
Ogac	1.84	0.22
immature	1.58	0.22
mature	1.88	0.22
Qasigialiminiq	2.05	0.10
immature	2.03	0.11
mature	2.06	0.10
Tariujarusiq	1.48	0.24
immature	1.62	0.23
mature	1.47	0.25

also significantly and drastically different from that derived from these data, a fact which must also be considered when comparing L-W relationships between these datasets.

Sex Ratios and Ages and Lengths at Maturity

Cod of both sexes matured at an age (3–5 years) and length (35.9–48.6 cm) that is moderate within the range known for the species throughout its geographic distribution (COSEWIC, 2003). Although the ages and lengths at maturity reported here were younger and shorter, respectively, than those that Patriquin (1967) reported for Ogac Lake (Table 7), some individuals in this study delayed maturation until quite advanced ages (9) and long lengths (73 cm).

The male:female sex ratios in 2003 were 0.40 in OG, 0.42 in QL, and 0.45 in TL. Patriquin (1967) described a shift in sex ratios towards females among older cod (M:F = 0.19 for cod aged 7 years or more, as opposed to 0.43 for cod younger than 8 years). In contrast, we found no difference in sex ratio between younger (< 8 years; M:F = 0.41) and older (> 7 years; M:F = 0.40) groups among cod collected in 2003. We did find a stronger shift toward females (0.50 to 0.39) between these same age categories in QL, but not in TL (0.45–0.46). For all three lakes, there were too few individuals in the tails of the age distributions to allow the change in sex ratio with age to be compared in a meaningful way.

TABLE 7. Age and length-at-maturity for each sex in each population, showing the age and length at 50% maturity, the oldest and longest immature cod, and the youngest and shortest mature cod.

Population	This study Ogac Lake		Patriquin (1967) Ogac Lake		Qasigialiminiq		Tariujarusiq	
Sex	M	F	M	F	M	F	M	F
Age at 50% maturity (years)	4.0	5.0	–	–	3.9	4.1	3.0	3.9
Oldest immature cod (years)	7	9	9	13	9	9	3	7
Youngest mature cod (years)	3	4	7	9	4	4	3	4
Length at 50% maturity (cm)	35.9	42.1	–	–	39.6	36.2	42.2	48.6
Longest immature cod (cm)	41.2	68.0	70	90	73	67.2	53.3	62.7
Shortest mature cod (cm)	31.9	36.2	60	80	42.4	43.7	41.7	40.2

Growth Characteristics

The growth rate parameter k was significantly greater in TL than in either OG or QL, indicating faster growth rates in TL. Despite a lower growth rate parameter, the VBGM predicted that OG cod will reach the same asymptotic length as cod from TL, because the asymptotic length parameter L_∞ of approximately 120 cm did not differ significantly between the two populations (Table 8, Fig. 9). By contrast, L_∞ was lower for QL than for OG or TL cod, although these differences were not statistically significant.

Patriquin (1967) interpreted the shift in sex ratios to favour females among older cod as an indication that males grew more slowly than females (so that large, cannibalistic females consume a greater proportion of the slower growing males). Although we found no such shift in sex ratio in the 2003–04 samples, the VBGM predicted that female cod in OG grow faster to a larger asymptotic size than males (Fig. 10), although the parameters of the VBGM did not differ significantly (Table 8). No such trend between the sexes of cod was apparent in QL or TL.

TABLE 8. Maximum likelihood comparison of the predicted von Bertalanffy mixed-effect growth curves fitted to individual back-calculated growth trajectory data for Ogac Lake, Qasigialiminiq, and Tariujarusiq.

	Parameter	Estimate	SE	df	p-value
QL-OG					
QL	$L_{\infty QL}$	91.99	6.95	113	
OG	$L_{\infty OG}$	101.64	8.34	113	0.2498
QL	k_{QL}	0.14	0.01	113	
OG	k_{OG}	0.16	0.01	113	0.3677
QL	t_{0QL}	-0.15	0.05	113	
OG	t_{0OG}	0.00	0.05	113	0.0045*
TL-OG					
TL	$L_{\infty TL}$	119.97	0.58	120	
OG	$L_{\infty OG}$	119.95	0.38	120	0.9530
TL	k_{TL}	0.16	0.01	120	
OG	k_{OG}	0.13	0.01	120	0.0014*
TL	t_{0TL}	-0.05	0.04	120	
OG	t_{0OG}	-0.09	0.04	120	0.3700
TL-QL					
TL	$L_{\infty TL}$	100.81	7.66	61	
QL	$L_{\infty QL}$	88.14	9.36	61	0.1808
TL	k_{TL}	0.19	0.02	61	
QL	k_{QL}	0.15	0.02	61	0.0297*
TL	t_{0TL}	-0.03	0.04	61	
QL	t_{0QL}	-0.12	0.06	61	0.1059
OG sexes					
OG_F	$L_{\infty F}$	96.98	6.45	831	
OG_M	$L_{\infty M}$	84.89	9.46	831	0.2018
OG_F	k_F	0.15	0.01	831	
OG_M	k_M	0.14	0.02	831	0.4215
OG_F	t_{0F}	0.00	0.03	831	
OG_M	t_{0M}	-0.08	0.05	831	0.0760

* Indicates a significant difference.

DISCUSSION

In general, differences in diverse aspects of the biotic and abiotic limnology of Ogac Lake, Qasigialiminiq, and Tariujarusiq appear to correspond to differences in measures of condition and growth characteristics among these cod populations. Particularly important differences appear to be the strong likelihood that OG receives significantly greater allochthonous influxes of marine nutrition than QL and TL and the absence of sea urchins in QL in contrast to their high abundance in TL.

Bathymetry and Limnology

Our measurements and observations suggest that OG receives greater influxes of allochthonous marine nutrition during inflowing spring tides (Hardie et al., 2008), which enter the lake with a greater frequency and volume than in TL or QL. These stronger influxes are due, in part, to the lower relative sea level of OG and to the nature of its connection to the sea (Hardie et al., 2008). Because summer habitat conditions of the seawater layer do not differ strongly among the three lakes (Hardie et al., 2008), the absence of urchins in QL cannot be readily explained.

The fact that cannibalism is much greater in OG than in TL is consistent with the high abundance of sea urchins in the latter, such that one would predict diminished reliance on cannibalism. Not surprisingly, sea urchins are about 50% more common in the stomachs of TL cod than in those of OG cod, and the consumption of coneworms is very low in TL. It is not clear, however, why cannibalism rates are not higher in QL. Given the lower-than-expected incidence of cannibalism in QL, and the absence of urchins, it is not surprising that clams and coneworms comprise a much larger portion of the diet in this lake relative to the other two. The only apparent advantage of these two prey choices

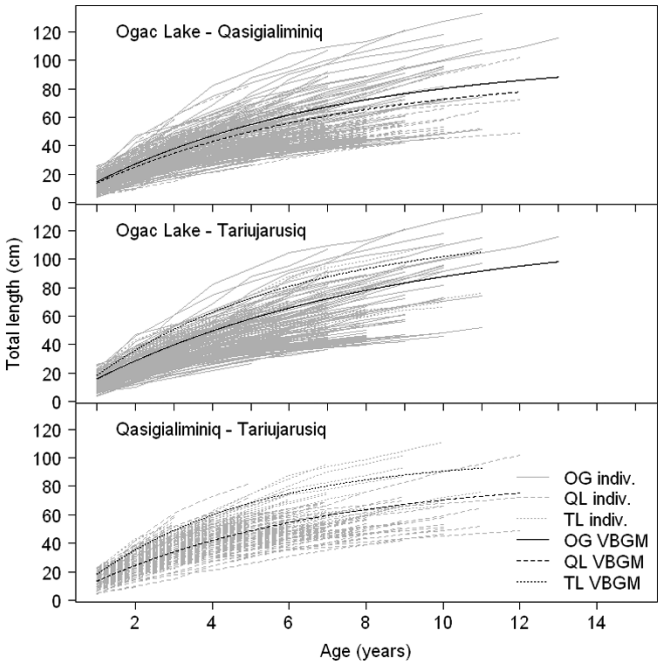

FIG. 9. Predicted von Bertalanffy mixed-effect growth models fit to individual growth trajectory data for Ogac Lake (n = 97), Qasigialiminiq (n = 100) and Tariujarusiq (n = 72).

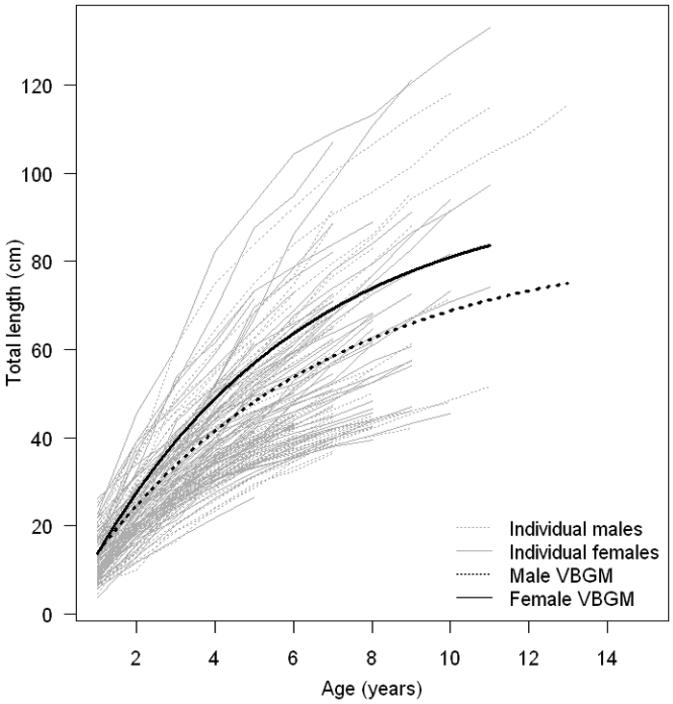

FIG. 10. Predicted von Bertalanffy mixed-effect growth models fit to individual growth trajectory data for male and female cod from Ogac Lake (2003).

is their perennial availability, because cod must forage for clams in a low-salinity environment, and for coneworms in deep waters that are hypersaline, acidic and anoxic, and lipid content is very low in both species. The length of about 60 cm at the onset of cannibalism is consistent with the mean lengths of cannibalistic Atlantic cod reported in the Baltic Sea (56 cm), where cod are apex predators, but lower than the mean of 85 cm reported for the species on the Spitsbergen Bank and off Newfoundland, where other large predators occur and where prey species diversity is greater (Juanes, 2003). Similarly, the absence of any other piscivore besides cod and the paucity of other prey species in the Arctic lakes probably contribute to the earlier onset of cannibalism.

It is important that not only can tidal influxes of nutrition be very abundant (Hardie et al., 2008), but the prey that they bring into the lakes are very rich in lipid energy compared to prey within the lake. This result highlights the possibility that these tidal inflows are of paramount importance to the short-term condition and long-term persistence of these cod populations. Both larval sculpin (which make up the largest part of the biotic content of tidal inflows) and cod larvae are found to be highly lipid-rich. As a consequence, cannibalism on larval cod (not quantified in this study) may represent a very important source of nutrition at various life stages, particularly for juvenile cod. However, we have not quantified the lipid content of zooplankton and benthic macro-fauna, which are also quite abundant. Other studies suggest that the lipid content of such prey items tends to be higher than even the most lipid-rich prey available in OG. For example, the most common Arctic copepod, *Calanus hyperboreus*, typically contains about 15% lipids by weight (Auel et al., 2003), and 5% is the estimated minimum for most marine plankton (Båmstedt, 1986). In summary, the stomach contents of cod in these three populations are consistent with what we would expect given qualitative observations of the prey available, the difficulty and stresses involved in obtaining these prey, and their relative energetic contents, with the proviso that we expected cannibalism rates to be higher in QL. These results further reinforce the hypothesis that measures of condition and growth rates are likely to be lowest in QL, where the frequency of empty stomachs is highest and cannibalism and prey diversity lowest (forcing cod to forage in physiologically stressful environments). Condition and growth rates are intermediate in TL, where cannibalism is low but prey diversity is moderate and likely less physiologically stressful to obtain, and highest in OG, where prey diversity and cannibalism are high, and tidal inflows more frequent and rich.

Length and Age Frequency Distributions

The shorter mean length of cod in QL relative to OG and TL is consistent with the observations of lower prey diversity (absence of sea urchins) in this lake, which may explain the observations of slower growth and shorter asymptotic length. The young mean age of TL cod is interesting, because mean length is quite high in this population, which is consistent with the observation of rapid growth to large size.

We cannot exclude the possibility that differences in age and length distributions among populations and among

sampling periods may reflect the movement over time of abundant cohorts within a population. In fact, there is some evidence that our samples are bimodal, consisting mostly of cod approximately 40–60 cm long, with a second mode of giant cod more than 100 cm long. This phenomenon is known from other fish populations (DeAngelis and Coutant, 1982; Griffiths, 1994; Hammar, 2000) in which a small number of individuals achieve giant sizes by making a transition to either intra- (Claessen et al., 2000) or inter-specific piscivory (Campbell, 1979).

We also cannot exclude the possibility that the non-random aspects of our sampling by angling may have contributed to the bimodality of the data. While it is certain that 40–60 cm length-class cod are very abundant in these populations, it is also true that the giant cod are extremely aggressive and perhaps disproportionately susceptible to angling. During angling and netting, we often observed giant cod attacking smaller cod, as well as biting the water probes and remote cameras being lowered into the water. These very large individuals are immediately attracted to any disturbances of the water, so their apparent relative abundance in the data (compared to circa 70–80 cm cod) may reflect their extremely aggressive nature and susceptibility to capture by angling.

Condition Metrics

Comparisons of condition metrics among these three populations, which were not sampled simultaneously, must be interpreted with caution given that condition indices are known to vary seasonally, usually increasing after spawning and throughout the growth season (Lambert and Dutil, 1997), when our sampling took place. It is noteworthy, however, that most cod in Arctic lakes exhibit summer HSI values of about 2% or lower, which may indicate that they are at or near total lipid depletion (Grant et al., 1998). At the other extreme, very high HSI values (22%) observed in some giant cannibalistic cod in these lakes exceed those previously observed in the wild and approach the highest values reported for the species in captivity (Jobling, 1988).

The exponent of the L-W relationship is especially high for cod from QL, indicating that they gain weight more rapidly as they lengthen than cod from the other two populations. The exponents of the L-W relationships for all three Arctic lacustrine populations are higher than the ones normally reported for this species, which usually more closely approximate isometry (2.92–3.14; www.fishbase.org). Several non-exclusive factors may explain why Arctic lacustrine cod populations, QL in particular, exhibit high length-weight relationship exponents. First, small cod may allocate more resources to increasing their length until they are long enough to be safe from cannibalism and then revert to allocating resources to weight increases. Differential growth allocation between length and girth is known to occur in other fish species when large piscivores are present (Holopainen et al., 1997). Second, smaller cod may experience poor condition because of difficulties in obtaining sufficient prey (foraging-risk, physiological stress, and low prey abundance or energy content), so that they are particularly "thin" early in life and can attain higher weights only when they have exceeded some length/age threshold that alleviates these stresses, or allows them to become cannibalistic, or both. This pattern may be particularly important in QL, where the absence of sea urchins may explain the poor condition of small cod. Discerning whether, and the degree to which, these phenomena are at play is not possible from our data, but both are consistent with increases in the weight-length relationship with age, particularly in QL. Certainly, this pattern is not unique to these Arctic lacustrine cod populations, but rather is characteristic of many fish populations, particularly when the realization of maturity results in relative weight increases (Roff, 1983).

Growth Comparisons among Populations

Relatively high variation in length-at-age among individuals exhibiting disparate growth trajectories, observed by Patriquin (1967) and confirmed here (Table 5), makes fitting growth curves to these data difficult in some cases. High growth-rate variability is not uncommon among fish populations in impoverished habitats (Nikolsky, 1963), particularly among high-latitude populations (Griffiths, 1994). This phenomenon will be addressed in detail in future work. In general, our results are consistent with the hypothesis that abiotic and biotic limnological conditions should result in the poorest growth conditions in QL, followed by TL and OG, except that growth rates are significantly higher in TL cod than in either of the other two populations. High sea urchin abundance may provide an abundant food source, particularly for smaller non-cannibalistic cod, while the low cannibalism rates may alleviate the foraging and growth costs of cannibalism avoidance, allowing for more rapid growth rates during early life than in OG, where cannibalism rates are much higher and urchin abundance is lower. Although OG cod have slower growth rates, they are predicted to reach the same or longer asymptotic length as TL cod, given a few extra growing seasons. The slower growth of young OG cod is consistent with more difficult growth conditions in OG for smaller cod (cannibalism avoidance, lower urchin abundance), although this difficulty would appear counter-intuitive given the rich tide-borne influxes of allochthonous nutrition. It is not surprising that QL cod, having the least abundant and least diverse prey, are the slowest growing and reach the smallest asymptotic size of the three populations.

Temporal Data from Within Populations

It is plausible that the substantial decrease in predation on sea urchins and concurrent increase in cannibalism observed in OG over the last half-century resulted from a decrease in urchin abundance. The most likely cause of a decrease in urchin abundance in OG over that period is the lowering of relative sea level by circa 35 cm in this region

(Doner, 2001), although it is less clear whether sea level lowering affects sea-urchin abundance via reduced immigration of urchin larvae during tidal inflows or via subtle changes in lake habitat. Despite the fact that our summer observations of habitat (salinity, dissolved oxygen, and temperature at depth) fall within the range reported throughout the open-water season during the earlier period (McLaren, 1967), increases in the relative abundance of freshwater diatoms in OG over the last 50 years suggest that the lake is freshening as relative sea-level drops in this area (Doner, 2001).

We can only speculate with regard to the change in the size range of cod cannibalized in this study from the range reported by Patriquin (1967). Our observation of much smaller victims of cannibalism (8.7 cm vs. Patriquin's 20 cm) is particularly noteworthy, whereas the upper extreme (36 cm vs. Patriquin's 40 cm) is less so. Beyond the possibility that this change is simply an artifact of limited lethal sampling in both studies, it is plausible that the more intense cannibalism on smaller cod in 2003–05 simply reflects differences in abundance of this size-class of cod relative to the size distribution of potential cannibal victims in the earlier study. The dynamics of cannibalism in monospecific fish systems often include periodic breakthroughs of larval cohorts that are otherwise suppressed by cannibalism (Bystrom, 2006). The change to smaller cannibalized cod could also be related to the shift from predation on sea urchins towards cannibalism mentioned above, especially if lower sea urchin abundance encouraged smaller cod to cannibalize even smaller prey.

Although the increase in the mean length of angled cod from OG from the 1950s to 1999–2003 is interesting, it is impossible to disentangle the factors which may be responsible. First, the angling equipment used in the present study may have been more suitable for catching large cod than the equipment used in earlier studies. Second, we cannot exclude the possibility that temporal differences in the abundance of giant cod are due to cyclic population dynamics, although the fact that the second "mode" of giant cod occurs around the same length in each instance suggests that this is an unlikely explanation. A suite of possible habitat changes may also contribute to changes in cod size, some acting to improve feeding and growth potential (e.g., longer season of tidal inflows, warmer climate) and others to degrade it (e.g., lower relative sea level, decreased sea-urchin abundance). What is perhaps most interesting is the concomitant dramatic increase in cannibalism. It is possible that decreased urchin abundance (assumed from cod diet changes) and the increased incidence and size-range of cannibalized cod have contributed to an increased abundance of giant cod.

The increase in the exponent of the length-weight relationship in OG between Patriquin's (1967) study and our work is also remarkable. This change in the ontogenetic pattern of growth suggests that present-day cod in OG grow "fatter" as their length increases than they did 50 years ago. Thus, survival may be more difficult than ever for small cod, but it becomes easier as their size increases. This difference may simply mean that each study sampled the OG cod population at a different point in a complex population dynamic cycle, reflecting the putative periodicity of cannibalistic populations known in other species. This trend is also consistent with our observation of increased cannibalism and a presumed decrease in availability of sea urchins, which could explain why smaller cod are in poorer condition and condition improves as cod get larger (and presumably more cannibalistic). Although such a change in the ontogenetic pattern of the L-W relationship could indicate changes in the onset of maturity, at which point energy is typically allocated away from somatic growth (length) in favour of reproductive tissues (adding weight), this explanation is unlikely, as we discuss below.

Contrary to our expectations, based on Patriquin's (1967) results and the presumption that the sub-optimal habitat at the northern extreme of the species' range would result in slower growth and later maturity, we found that maturity in all three populations is near the average for the species, which ranges from 2 to 7 yr. (COSEWIC, 2003). Two possible explanations for the difference between Patriquin's (1967) and our estimates of age-at-maturity are related to methodological error. First, we observed during our fieldwork that the gonads of smaller cod were generally in a later stage of post-spawn recovery than those of the larger cod, which appeared to have spawned earlier in the season. As a result, we speculate, if only because we initially made the same error, that recently spawned smaller cod may have been misclassified as immature in Patriquin's study. Fortunately, we took digital photographs of every gonad for verification at a later date. Second, Patriquin's age estimates for a given length are markedly older than those from this study, which suggests inconsistency between studies in aging methods. Unfortunately, neither the original otoliths nor the raw length-at-age data from Patriquin's (1967) study are currently available for re-examination or analysis.

The fact that sex ratios did not change over the length-range of cod in our data, in contrast to the important difference reported by Patriquin (1967), may be an artifact of small lethal samples. In any case, Patriquin's (1967) speculation—that the shift towards female abundance at larger sizes may have been due to greater growth rates among females than males—was supported by our analysis for the Ogac Lake population, but not for the other lakes, where cannibalism rates are much lower. This result is consistent with Patriquin's explanation and also with well-known differences in growth and asymptotic size among many fish species, often favouring females.

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